# ON DEVELOPMENTAL PATTERNS OF OPISTHOBRANCHS

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## ABSTRACT

Data from recent publications on developmental characteristics of opisthobranchs are added to prior compilations to arrive at a broad picture of opisthobranch developmental patterns. Egg diameters vary from 40 to 380 $\mu$m, with a modal size of about 75 $\mu$m; this distribution is similar for each of the larger opisthobranch orders alone. In general, planktotrophic larvae arise from eggs smaller than 130 $\mu$m, but a few species with lecithotrophic larvae or even directly developing juveniles fall below this limit. Lecithotrophic larvae develop from eggs as large as 220 $\mu$m, but most from eggs less than 185 $\mu$m in diameter. All larger eggs produce crawling juveniles at hatching. Positive correlations link egg size and hatching-shell size, but there is no correlation between hatching size and settling-shell size nor hatching size and larval duration. Type II larval shells are larger than Type I shells from eggs of equal diameter. Until metamorphic competence, the duration of larval existence is temperature dependent for both larval types, and for planktotrophic larvae is effected by phytoplankton abundance. Once larvae are metamorphically competent, the duration of their larval period is determined by the availability of appropriate settlement substrata.

Size of recently metamorphosed juveniles shows low correlation with egg diameter ($r^2 = 0.29$), but does not exceed 500 $\mu$m length for any species with larval development, whether planktotrophic or lecithotrophic. Only direct development with little retention of larval characters produces hatching juveniles between 0.5 and 1.0 mm long. We conclude that opisthobranch larval development is regulated by strong phylogenetic constraints and that selective pressures leading to non-planktotrophic development have probably not been the same across all opisthobranch taxa. Early juvenile mortality can be a strong force favoring high larval numbers, even in species with lecithotrophic larval development.

The ecology and evolutionary patterns of reproduction and development in opisthobranchs have been the subject of intense interest in recent years, as reflected by the number of general reviews of the subject that have appeared (Thompson, 1976; Bonar, 1978; Hadfield, 1978; Hadfield and Switzer-Dunlap, 1984; Todd, 1981, 1983). Our goal here is not to analyze again all the material covered by the recent reviews, but rather to focus on the developmental patterns, or modes, exhibited by opisthobranchs and to attempt to arrive at generalizations regarding their evolutionary implications and limitations. In so doing, we have updated and utilized the data base compiled from the literature by Hadfield and Switzer-Dunlap (1984). Only publications not included in the earlier bibliography are cited in the present paper. Species not considered by Hadfield and Switzer-Dunlap are listed in Table V. Several important points must be made about the data set. (1) The literature is variable in its reliability. Authors often differ in their reporting of egg diameters and other developmental parameters for the same species. Occasionally, from paper-to-paper, even single authors give widely differing numbers. (2) We have used some data in ways authors never intended. For instance, we have extrapolated measurements from drawn and photographed figures, often when the figures didn't include clear magnification scales and they had to be deduced from the texts. (3) Not all parameters mean the same thing in all taxonomic groups; juvenile length (used as a measure of post-metamoprhic size) is elastic and may represent a very different proportion of body mass in different opisthobranch taxa. (4) Where authors gave only ranges for parameters of interest (e.g. egg diameter, rearing temperature) we have substituted a single mid-point value. (5) For eight species, different authors have presented very

different data for species of the same name; we have considered these to be separate species in our analyses. (6) We have selected references that provided the most complete information about each of the 418 species of opisthobranchs considered in this review. Thus some published data for a species may have been utilized and other data not. It is hoped that the large sample sizes available for some of these parameters (e.g. egg diameters were available for 369 species) more than outweigh the effects of these numerous sources of uncertainty.

As has often been stated, benthic marine invertebrates achieve recruitment to juvenile-adult populations in three basically different ways. First, there are those species that release their young as swimming larvae which must feed for some period of time in the plankton before they are competent to assume the adult form and habitat. These are generally referred to as "planktotrophic-pelagic", "indirect-planktotrophic", etc. Second are species which reproduce as above, except that their larvae, which usually swim for a short period of time before assuming the adult habitat and form, do not need to feed before metamorphosing; we refer to these species variously as ones with "indirect-lecithotrophic development" and "pelagic-non-feeding larvae." Finally, there are those species which release their young as small replicates of themselves, directly into the parental habitat. This mode of reproduction, usually referred to as "direct development", could be accomplished by viviparity, ovoviviparity, brooding, or depositing zygotes in external capsules for development. The second group, the lecithotrophic larviparous forms, overlap both of the others: the direct developers in not requiring external nutrition to achieve the benthic stage (in fact the direct developers, too, are lecithotrophic), and the planktotrophs in having a genuine larval stage that must find a habitat suitable for metamorphosis, growth and reproduction.

The successful result of the developmental process for any species is the production of a juvenile organism, usually residing in the definitive habitat of the species. Thus one measure of evolutionary success is how assuredly a species accomplishes this event. The time required to reach the juvenile stage varies among these developmental modes in several ways, the first being the time spent in pre-hatching development. This period is generally shortest for the planktotrophic forms and longest for the direct developers. The duration of pre-hatching development varies with egg size (the larger the egg, the longer the pre-hatching period) and with temperature (the colder the temperature, the longer the pre-hatching period).

The duration of pre-juvenile development also varies during the larval phase. This phase is longest for the planktotrophs, is usually much less for the pelagic-lecithotrophs, and is non-existent for the direct developers. For both pelagic groups, the duration of the planktic period is sensitive to temperature, and for the planktotrophic forms, duration is also affected by food quality and abundance.

The generalizations so far outlined pertain to nearly all marine invertebrate groups. Our goal here is to look specifically at the opisthobranch mollusks and attempt to arrive at explanations for the differing durations of development, as well as to produce some generalizations about how pelagic larvae find their prospective juvenile habitats.

## WHERE LARVAE SETTLE

Before discussing "when larvae settle", we first consider where larvae settle, partly because it is simpler to address and partly because it contributes to an understanding of the first question. In this discussion we deal only with species that actually have a larva, either planktotrophic or lecithotrophic. Species with direct development will obviously "settle" in the place where they hatch, presumably in the same habitat where their parents existed and deposited their eggs.

It is axiomatic that for a larva to survive and grow to a successfully reproducing adult, it must settle and metamorphose in a place where: (1) food is available, (2) there is refuge from predators, and (3) others of its kind are around with which to mate. Usually such habitats are narrowly and discontinuously distributed in the sea, so that a larva must be able to locate and recognize them at a time when it is capable of metamorphosing. This is accomplished in most opisthobranch larvae through a developmental-behavioral shift that brings about swimming near the bottom (e.g. Miller and Hadfield, 1986) and then by sensing chemical and/or physical attributes of appropriate sites, settling onto such sites and metamorphosing there (Hadfield and Scheuer, 1985).

The degree of specificity of the settlement cue has been found to vary considerably, but, in a general sense, predictably (see Tables 1 and 2), as follows. Species with highly specific food requirements (i.e. feeding on only one or a small group of species) which are sessile and patchy in distribution, will metamorphose only in response to chemical cues arising from the food substance, usually a colonial animal or an alga. Examples include coral-, hydrozoan-, and bryozoan-feeding nudibranchs, and algal-feeding sacoglossans and sea hares. Species with either less specific food requirements or motile prey usually settle in response to general characteristics of the environment in which their prey and other members of their own species live. Examples include carnivorous cephalaspideans and several aeolid nudibranchs that feed on a variety of fouling community organisms [*Hermissenda* ( = *Phidiana*) *crassicornis* (Eschscholtz)] is a good example (Harrigan and Alkon, 1978).

Both soluble chemical cues and absorbed ones requiring larval contact have been implicated in inducing settlement and metamorphosis in different opisthobranch species. In our laboratory, work has focused on the settling requirements of the coral-feeding aeolid nudibranch, *Phestilla sibogae* Bergh. Lecithotrophic larvae of this species settle only in response to a soluble chemical cue emanating from the adult prey, members of the scleractinian coral genus *Porites*. The inducing substance is a small (<500 dalton), water soluble molecule (Hadfield and Scheuer, 1985). It is constantly leaching from the coral in the field, but is probably concentrated enough to elicit metamorphosis only in the coral heads themselves. To our knowledge, no other opisthobranch

**Table 1.** Settlement requirements of opisthobranchs with planktotrophic larvae.

| Species | Adult Food | Settlement Requirement | Reference |
|---|---|---|---|
| **Nudibranchia** | | | |
| **Doridacea** | | | |
| *Doridella obscura* Verrill | *Electra crustulenta* (Pallas) | same[1] | Perron and Turner (1977)[2] |
| *D. steinbergae* (Lance) | *Membranipora villosa* Hincks | same | Bickell and Chia (1979)[2] |
| *Onchidoris bilamellata* (Linnaeus) | barnacles | same | Todd (1981)[2] |
| *O. muricata* (Müller) | *E. pilosa* (Linnaeus) | same | Todd and Havenhand (1985) |
| *Archidoris pseudoargus* (von Rapp) | *Halichondria panicea* (Pallas) | same | Todd and Havenhand (1985) |
| *Rostanga pulchra* MacFarland | *Ophlitaspongia pennata* (Lambe) | same | Chia and Koss (1978) |
| **Aeolidiacea** | | | |
| *Phidiana crassicornis* (Eschscholtz) | various cnidarians and tunicates | *Obelia* spp. | Harrigan and Alkon (1978) |
| *Phestilla melanobranchia* Bergh | *Tubastraea coccinea* Lesson | same | Harris (1975)[2] |
| **Dendronotacea** | | | |
| *Melibe leonina* (Gould) | various crustaceans, etc. | surface | Bickell and Kempf (1983) |
| *Tritonia diomedea* Bergh | *Virgularia* sp. and other pennatulaceans | surface (enhanced by *Virgularia* sp.) | Kempf and Willows (1977)[2] |
| **Cephalaspidea** | | | |
| *Acteocina canaliculata* (Say) | ? small molluscs | surface | Franz (1971)[2] |
| *Haminoea solitaria* (Say) | uncertain; microalgae? molluscs? | 1° film from adult habitat | Harrigan and Alkon (1978)[2] |
| **Sacoglossa** | | | |
| *Alderia modesta* (Lovén) | *Vaucheria* sp. | ? surface +/- *Vaucheria* | Seelemann (1967)[2] |
| *Elysia chlorotica* (Gould) | filamentous green algae | ? | Harrigan and Alkon (1978)[2] |
| **Anaspidea** | | | |
| 9 Aplysiid species | each specific to a few algae | same | Switzer-Dunlap and Hadfield (1981) |

[1]settlement substratum is the same as adult food; [2]cited in Hadfield and Switzer-Dunlap, 1984.

settlement factor has been explored as to its chemical structure, but evidence appears to implicate non-soluble cues in other species (e.g. *Rostanga pulchra* MacFarland; Chia and Koss, 1978). Numerous studies on *Aplysia* species in our lab have failed to produce evidence for soluble inducer molecules (unpublished data).

Evidence gained from studies on *Phestilla*, as well as on other marine gastropods (e.g. the abalone; Morse *et al.*, 1980) and members of other phyla (sea urchins, for instance), strongly implicates specific external larval receptors that are activated by specific chemical substances in the environment by molecular fitting ( the hormone-receptor model fits well). Once larval receptors are activated, the signal is transmitted by neural pathways (excess potassium alone can induce many invertebrate larvae to metamorphose), and the morphogenetic events of metamorphosis result from the action of well known neurotransmitter- and hormone-like substances (choline-containing compounds and catecholamines) on transforming tissues (Hirata and Hadfield, 1986; Yool *et al.*, 1986).

Larvae that respond to general cues have been reported to require either: (1) only a solid surface upon which to metamorphose; (2) a surface coated with a so-called primary film of marine bacteria and fungi and their extracellular exudates; or (3) a surface plus a primary film derived from micro-organisms specific to the appropriate adult habitat (Tables 1 and 2). It is doubtful if any larvae metamorphose on genuinely clean glassware, and probably most larvae observed to metamorphose in culture were doing so in response to at least a primary film; such films develop in less than 24 hours in sea water, particularly in warmer waters (Zobell and Allen, 1935).

All species have been evolutionarily molded to assure that their offspring that survive to metamorphic competence have a good chance of correctly finding a habitat appropriate for juvenile survivorship. The time required for development from egg to settled juvenile is strongly dependent on the mode of development. Thus in the following section, we examine developmental mode as a guide to understanding the duration of development in opisthobranchs. Since direct

**Table 2.** Settlement requirements of opisthobranchs with lecithotrophic larvae.

| Species | Adult Food | Settlement Requirement | Reference |
|---|---|---|---|
| Nudibranchia | | | |
| Doridacea | | | |
| *Adalaria proxima* (Alder and Hancock) | *Electra pilosa* and other encrusting Bryozoa | *Electra pilosa* | Thompson (1958)[2] |
| *Discodoris erythraeensis* Vayssiere | fine algae and diatoms | surface | Gohar and Aboul-Ela (1959)[2] |
| *Hoplodoris nodulosa* (Angas) | sponges | surface | Rose (1983) |
| Aeolidiacea | | | |
| *Eolidina mannarensis* Rao | probably hydroids | surface | Rao and Alagarswami (1960)[2] |
| *Eubranchus exiguus* (Alder and Hancock) | *Kirchenpaueria pinnata* (Linnaeus) (Hydrozoa) | same[1] | Tardy (1962)[2] |
| *E. farrani* (Alder and Hancock) | *Aglaophenia pluma* (Linnaeus) and other hydroids | *Obelia geniculata* (Linnaeus) | Todd (1981) |
| *Cuthona adyarensis* Rao | *Bimeria* sp. and *Laomedea* sp. (Hydrozoa) | algae, etc. | Rao (1961)[2] |
| *Phestilla sibogae* Bergh | *Porites* spp. (Scleractinia) | same | Hadfield (1977)[2] |
| *Tenellia pallida* (Nordmann) | *Laomedea loveni* (Allman) and other hydroids | surface | Rasmussen (1944)[2] Eyster (1979)[2] |
| Dendronotacea | | | |
| *Tritonia hombergi* Cuvier | *Alcyonium digitatum* (Linnaeus) | same | Thompson (1962)[2] |
| Sacoglossa | | | |
| *Berthelinia caribbea* (Edmunds) | *Caulerpa verticillata* (Agardh) | same | Grahame (1969)[2] |
| *B. limax* Kawaguti and Baba | *C. okamurai* (Webber-Van Basse) | ? | Yamasu (1969)[2] |
| Notaspidea | | | |
| *Berthellina citrina* (Rüppell and Leuckart) | probably ascidians | surface | Gohar and Aboul-Ela (1957)[2] |

[1]settlement substratum is the same as adult food; [2]cited in Hadfield and Switzer-Dunlap, 1984.

developers place their juveniles directly into a habitat that the previous generation had already found to be salubrious, we conclude by looking to them to understand one of the primary questions of this essay: "When do larvae metamorphose?"

## EGG SIZE AND DEVELOPMENTAL MODE

It has been traditional when comparing the three typical developmental modes of opisthobranchs or other marine invertebrates, pelagic-planktotrophic, pelagic-lecithotrophic and direct, to assume that they are three different means to the same end. In its simplest definition, that end is a metamorphosed juvenile in a habitat suitable for growth, survival and reproduction, and the major difference in the modes of development is the amount of energy packed into each ovum. This traditional view usually invokes "pie arguments." The components of these arguments are (1) across species there is a set amount or proportion of energy available for reproduction ( = the pie) and (2) the number of offspring produced at birth is a function of how large each ovum is made ( = the number of slices into which the pie is

cut). When applied to larval biology, the pie arguments predict that, in general, small eggs result in small larvae which must feed in the plankton and grow to a size equal to that achieved at birth when the pie is sliced into fewer but larger pieces as in lecithotrophic and direct development. That is to say, all modes of development should produce settled juveniles of about the same size (e.g. Strathmann, 1978a, 1985).

We can now ask, is the prediction of uniform settling sizes across developmental modes valid for opisthobranchs? To answer this question we must examine a large amount of data that will allow us to compare egg sizes with juvenile sizes across developmental modes. The first step is to look at the distribution of egg sizes among opisthobranchs of different developmental modes to determine if egg size is smaller among species with planktotrophic development than among those with lecithotrophic-pelagic and direct development. Average egg diameters for pelagic-planktotrophic, pelagic-lecithotrophic and direct developers are 84 $\mu$m, 143 $\mu$m, and 200 $\mu$m, respectively. The differences are significant for planktotrophic eggs when compared to either of the other two modes (planktotrophic vs. lecithotrophic, t = 8.355, P < 0.001; planktotrophic vs. direct, t = 9.171, P < 0.001),

and for the mean size of lecithotrophic-pelagic eggs compared to that of direct developers (t = 3.971, P < 0.001).

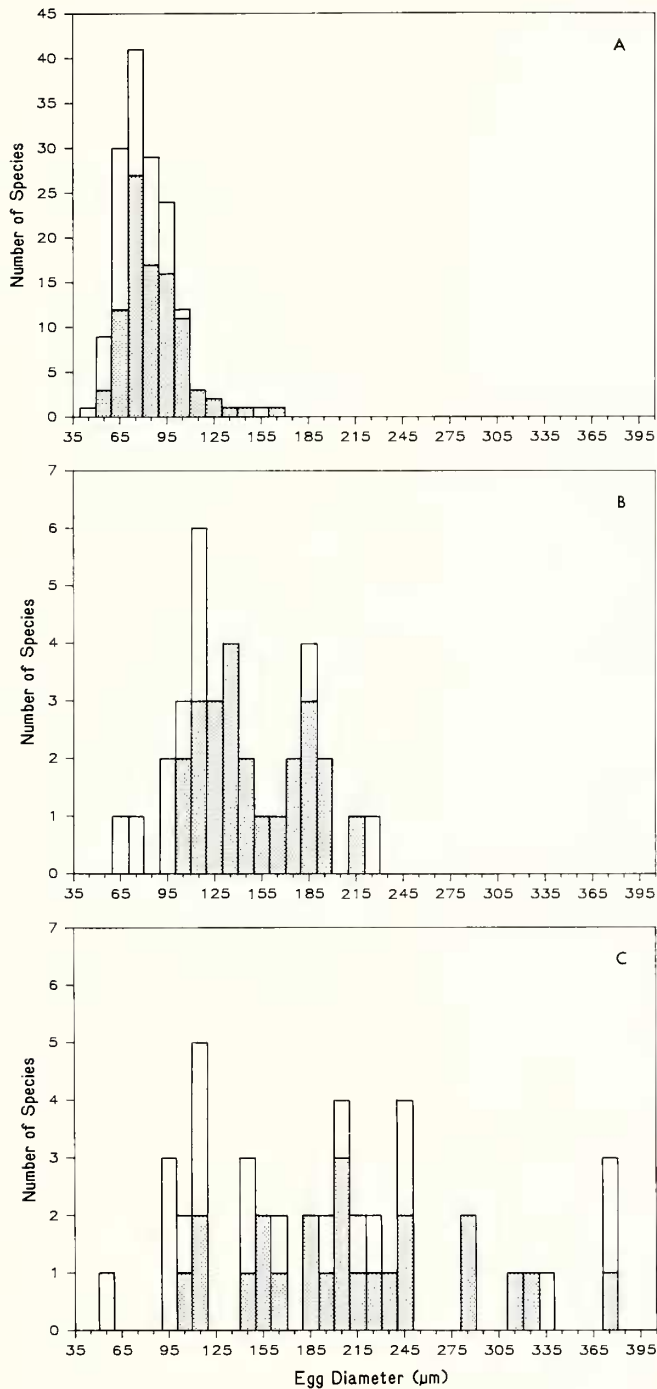Figure 1A displays egg-size distributions among opisthobranchs with planktotrophic larvae. It should be noted, (1) that the majority of species fall into a rather wide range of 45 to 130 μm diameter ova, (2) that the modal size, about 75 μm, is set by the most abundantly measured group, the Nudibranchia, and (3) that the eggs of Sacoglossa tend to be smaller (see Fig. 7).

The distribution of egg diameters in opisthobranch species with pelagic-lecithotrophic development is displayed in figure 1B. It is clear that the range of sizes is larger than for planktotrophic species; egg diameters fall between one hundred and two hundred microns. Again, it is notable that sacoglossans achieve lecithotrophy at smaller egg diameters (mean = 97 μm; n = 9), as previously noted by Clark and Jensen (1981).

Finally, the ova of species with direct development clearly achieve the largest sizes of all, with a range of diameters extending from 120 to 380 microns (Fig. 1C). These ova broadly overlap the sizes of planktic-lecithotrophs and extend to much larger sizes. In the direct developers with
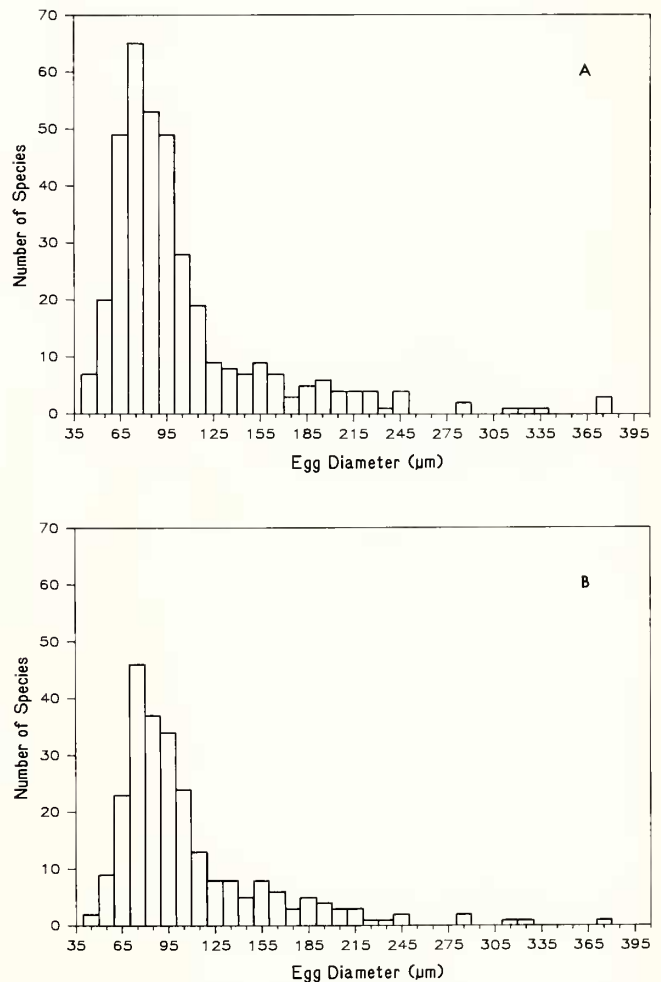


Fig. 1. Egg-size distribution in Opisthobranchia. **A.** Species with planktotrophic larval development. Hatched bars, Nudibranchia (n = 94); open bars, all other orders (n = 61). **B.** Species with lecithotrophic larval development. Hatched bars, Nudibranchia (n = 24); open bars, all other orders (n = 10). **C.** Species with direct development. Hatched bars, Nudibranchia (n = 23); open bars, all other orders (n = 20). (Note different vertical scales.)



Fig. 2. **A.** Egg-size distribution in all Opisthobranchia (n = 369). **B.** Egg-size distribution in the Nudibranchia (n = 250).

smaller eggs, the clarity of mode is weakest. Many of these metamorphose at about the time of hatching, and some are even mixed, with some larvae metamorphosing in the egg jelly and others after a brief swim. Evolutionarily, these might be construed as species in transition from indirect to direct development.

We next examine the relative distributions of egg sizes among opisthobranchs. In figure 2A the frequency distribution of egg diameters across all opisthobranchs is plotted. It can be seen that (1) the range is wide, 40-380 $\mu$m, but (2) most ova fall into the narrow range of 60-110 $\mu$m, and (3) the basically unimodal distribution (with the mode about 75 $\mu$m) is skewed, with a long "tail" stretching out to the right. The same trends hold for successively smaller taxonomic units; similar data are plotted for the order Nudibranchia in figure 2B, for the nudibranch suborders Doridacea and Aeolidacea in figures 3 and 4, and for the families Dorididae and Chromodorididae in figures 5 and 6. Sacoglossa (Fig. 7) show a trend to smaller ova; these data are dominated by
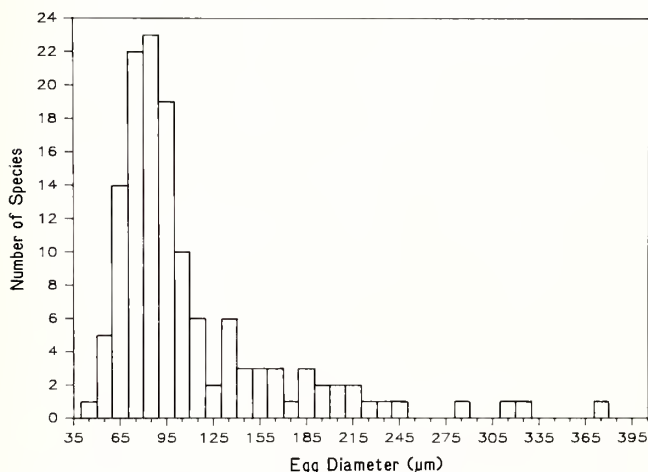


**Fig. 5.** Egg-size distribution in the nudibranch family Dorididae (n = 24).

measurements made by Clark and co-workers on the Florida-Caribbean fauna, and it would be interesting to know if sacoglossans produce similarly small ova throughout world seas. The relatively small egg diameters seen in the modal size classes of all groups are strongly indicative of the dominance of the feeding larva in opisthobranch development (see below).

Table 3 summarizes information gleaned from the literature on the numbers of species with different developmental modes in most opisthobranch orders. Species whose egg diameters were presented in the literature, but whose developmental modes were not stated, are included as an extra column. While most, if not all, of these probably have pelagic-planktotrophic development, they are not included in that category due to uncertainty. Judging strictly from the designated data, about 67% of all species studied have planktotrophic larvae, with the lecithotrophic-larval and direct modes accounting for about equal portions of the remainder. If, however, the uncertain species (column 5) are assumed



**Fig. 3.** Egg-size distribution in the nudibranch suborder Doridacea (n = 134).
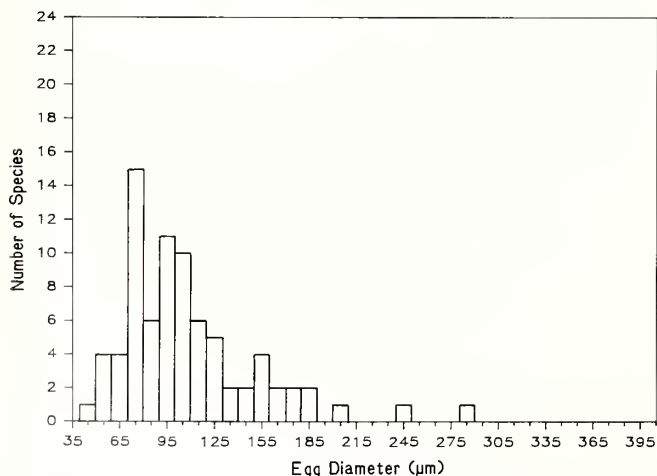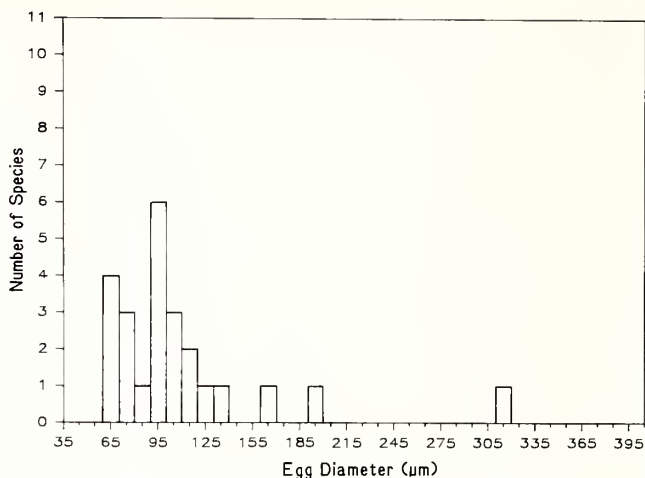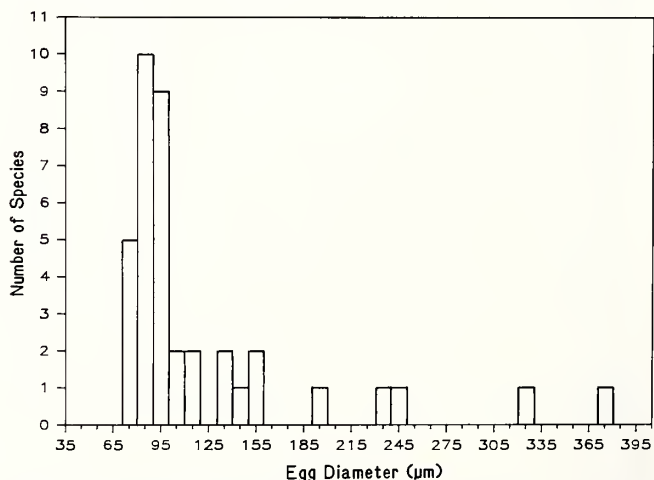


**Fig. 4.** Egg-size distribution in the nudibranch suborder Aeolidacea (n = 79).



**Fig. 6.** Egg-size distribution in the nudibranch family Chromodorididae (n = 38).
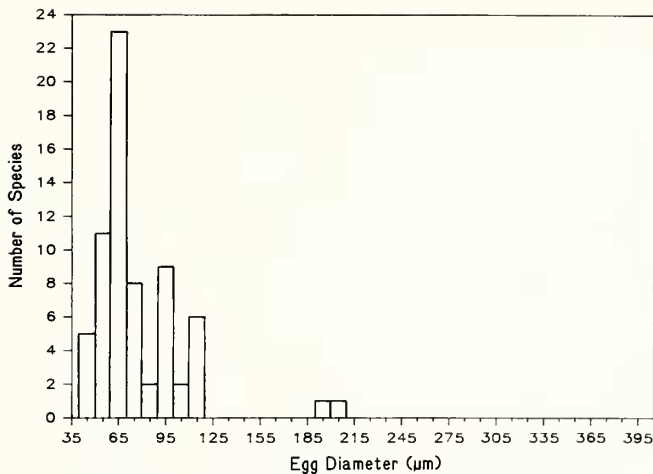
**Fig. 7.** Egg-size distribution in the order Sacoglossa (n = 68).

to have feeding larvae, the percentage of this type jumps to about 80%. Certainly this mode is by far the most abundant among opisthobranchs, a generalization that appears to hold for each of the major orders. From the data summarized in figures 1-7 and Table 3, we conclude that (1) egg size clearly distinguishes species with feeding larvae from those with non-feeding developmental modes (lecithotrophic-pelagic and direct) and (2) most opisthobranchs produce small eggs that develop into planktotrophic larvae.

**Table 3.** Developmental patterns in opisthobranchs.

| Order | No. Spp. w/Plankto- trophic Dev. | No. Spp. w/Lecitho- trophic Dev. | No. Spp. w/ Direct Dev. | Egg Diameter only |
|---|---|---|---|---|
| Nudibranchia | 100 (66%) | 27 (18%) | 24 (16%) | 109 |
| Cephalaspidea | 16 (70%) | 0 | 7 (30%) | 1 |
| Sacoglossa | 31 (63%) | 8 (16%) | 10 (20%) | 20 |
| Anaspidea | 17 (89%) | 0 | 2 (11%) | 0 |
| Notaspidea | 0 | 2 | 0 | 4 |
| "Pteropods" | 4 (67%) | 0 | 2 (33%) | 3 |
| TOTAL | 168 (67%) | 37 (15%) | 45 (18%) | [137] |

## IS THE TIMING OF METAMORPHOSIS SIZE DEPENDENT?

Egg size is a relatively good predictor of hatching shell size in opisthobranchs (Fig. 8): the larger the egg, the larger the shell size at hatching. Figure 9 shows that the generalization is quite sound for Nudibranchia alone and an additional important point. Shells of Type II (egg-shaped, inflated larval shells that do not grow during larval development) are much larger than Type I shells (coiled shells which do grow during development) arising from eggs of the same size (opisthobranch larval shell types are discussed by Thompson, 1961). This is probably related to the fact that space for body growth is included inside Type II shells, while it can be provided only by incremental growth in Type I shells. It can

be further concluded from figure 10 that the relationship between egg size and hatching shell size is consistent even among smaller opisthobranch taxa (the nudibranch superfamily Doridacea and the family Chromodorididae). Due to the fact that a larval shell does not appear during the ontogeny of opisthobranchs with ametamorphic direct development, these opisthobranchs add nothing to understanding the egg-size:shell-size relationship.

If the hypothesis is valid that settlement is optimized at about the same size among related species, then predictions relating egg size (the equivalent of hatching size; Figs. 8-10) to larval period should hold. Because the amount of growth during the pelagic period of planktotrophic species is positively related to the duration of the pelagic period (see Hadfield and Switzer-Dunalp, 1984: Fig. 39), the duration of the pelagic period should correlate negatively with egg diameter; it can be seen from data in figure 11 that it does not. In fact, there is no clear relationship between hatching size and settling size, a point illustrated in figure 12.

Additionally, if there was an optimal settling size for species with lecithotrophic development, one would expect that all eggs producing lecithotrophic larvae would be of a similar size, which they clearly are not (Fig. 1B, 11), even within restricted taxonomic groups. Egg diameters range from under 100 $\mu$m to over 200 $\mu$m for lecithotrophic nudibranchs (n = 24), from 110 to 185 $\mu$m for lecithotrophic aeolidaceans (n = 15), and from 69 to 120 $\mu$m for lecithotrophic members of the order Sacoglossa (n = 8). It is possible that within highly restricted taxa such as families or genera, trends toward more uniform settling sizes may occur, but this is not obvious from currently available data.

Can we predict the mode of development of an opisthobranch species by examining characteristics of its biology other than egg diameter? Using the pie arguments, the most usual approach has been to attempt predictions based on adult energetics. The assumption, as stated previously, is that the energy available for reproduction will be a constant amount or proportion as one compares across species with different developmental modes. This has not turned out to be true (see Strathmann, 1985, for a discussion covering all types of invertebrates). Chia (1971), studying three sympatric sacoglossans with differing developmental modes, found that the amount of egg protoplasm produced differed greatly among the species. A species with planktotrophic larvae [*Limapontia capitata* (Müller)] produced nearly three times as much "egg protoplasm" as a directly developing species of about the same animal size (*Acteonia cocksi* Alder and Hancock). Todd (1979) compared two sympatric nudibranchs, one with planktotrophic and the other lecithotrophic pelagic development and found the caloric investment in ova to be greater in the lecithotrophic species, but the relative reproductive effort (dry weight of spawn divided by body dry weight) to be greater in the planktotrophic species. Sarver (1978) conducted experimental studies of reproductive effort (RE) in the anaspidean *Aplysia juliana* Quoy and Gaimard and found that RE varied over the lifespan of individuals and as a result of the amount of food eaten. These shifts were seen whether RE was measured as the
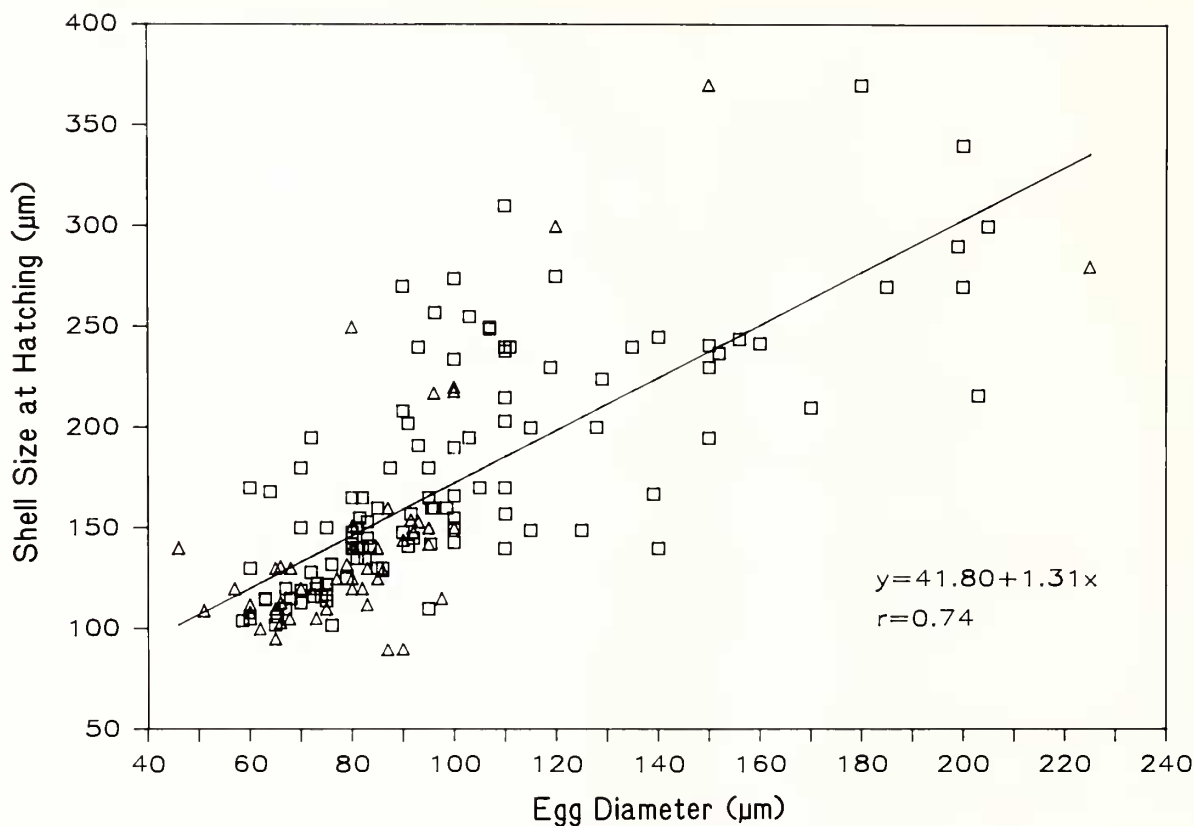
**Fig. 8.** Larval-shell length at hatching vs. egg diameter. □, Nudibranchia (n = 113); △, all other orders (n = 53). The cephalaspidean *Philine gibba* Strebel, egg diameter 379 μm, hatching size 375 μm, is not included.

percent of maximum body weight represented by the weight of all spawn produced during life, or as total calories spawned expressed as a percent of total calories ingested. Reproductive effort measured as weight was 135% for animals on *ad libitum* ration and about half that if provided with only three-quarters of the *ad libitum* amount. Expressed as calories, RE was 10.69 for *ad lib* ration and 7.25 for 75% ration. Because animals found in the field never achieved the size of *A. juliana* reared in the laboratory with an *ad libitum* food supply, Sarver concluded that the food regime of this animal is restrictive and that RE *in the field* must vary in time and space. It thus appears that there are no generalizations to be drawn relating reproductive energetics to developmental mode that can apply throughout the Opisthobranchia, and RE is not a useful predictor of developmental mode.

The absence of a correlation between egg size (thus hatching size) and settlement size and the lack of usefulness of reproductive effort in predicting developmental mode indicate that there are flaws in the original assumptions of the pie arguments, at least in application to most opisthobranchs. In addition to the absence of consistency in reproductive effort across or within developmental modes, it appears that another basic problem lies in the prediction that benthic juveniles resulting from all modes should be about the same size, at least within restricted taxa or ecological types (for example sponge feeders). We showed above that settling larval *shell* sizes differed among opisthobranchs with the same

and different developmental modes, and we next examine the assumption that different modes of reproduction produce similarly sized benthic juveniles (i.e. shortly after metamorphosis). Here shell measurement is discarded except for groups like cephalaspideans where it could be a good measure of juvenile size. Examing juvenile size rather than shell size seems particularly important for the nudibranchs where the two different shell types have such different relationships with egg diameters (Fig. 9), and because all nudibranchs (which are the source of most data) and most sacoglossans shed their larval shells at metamorphosis, making shell measurements poor approximations of the size of newly metamorphosed juveniles.

The data presented in figure 13 reveal some rather surprising and, to us, not intuitive conclusions. First, as previously shown, planktotrophic larvae all arise from small eggs, with essentially no overlap with the other two modes of development. Secondly, although lecithotrophic larvae arise from larger eggs, there is a limit to size of the juvenile that results from pelagic development that is common to both pelagic modes; the limiting size is a juvenile about 500 μm long. Third, while there is a broad overlap of egg sizes between pelagic-lecithotrophic and direct developers, only some direct developers "escape" the juvenile size limitation of ~500 μm to produce very large juveniles, some of them up to a millimeter long. Most of the distribution of juvenile sizes among direct developers can be explained by the two pat-

terns of development known in this group: metamorphic-direct developers (a shelled, veliger stage occurs within the egg mass) and ametamorphic-direct developers (a shell and most other vestiges of the veliger are lacking in their ontogeny) (see Bonar, 1978, for a discussion of these two modes). The ametamorphic direct developers are indicated by filled triangles in figure 13; resulting juveniles are clearly larger. These can be considered the most evolved in the direction of direct development. We conclude that the presence of a larval shell sets a maximum size limit on opisthobranch juveniles, a limit that doesn't exist, at least at such a small size, among prosobranchs.

The great spread in juvenile sizes and the apparent relationship between juvenile size and developmental mode might be due to mis-interpretation of existing data since different types of opisthobranchs have different length-to-weight ratios; only good weight measurements of newly metamorphosed juveniles would resolve this problem. On the other hand, juvenile length could provide a valid measure of size as it relates to predator avoidance. For some species, factors unrelated to selection for juvenile size might relate developmental mode to different aspects of their biology; one is adult size (Menge, 1975; Strathmann and Strathmann, 1982). Arguments relating adult size to developmental mode have been devoted to brooding, a habit unknown for opisthobranchs (with a possible exception cited by Rose and Hoegh-Guldberg, 1982). The arguments assume that small animals,

having an absolute (and small) limit on the amount of energy available for reproduction must take the "safer" path of direct development, by-passing the plankton as a source of nutrition and dispersal to avoid it as a great source of developmental mortality. Table 4 lists directly developing species for which we could find data on adult lengths as well as juvenile lengths. It is clear that both large and small species produce large eggs that develop directly into hatching benthic juvenile stages. Still, reduction in adult size may have driven selection for direct development in some species.

Another possibility, alluded to above, is that certain ecological conditions could predicate different "best sizes" after metamorphosis. This hypothesis defies clear testing, but at least among specialized feeding groups (e.g. sponge feeders; hydrozoan feeders; bryozoan feeders) no generalizations about optimal juvenile sizes emerge from our data set. A wide range of juvenile sizes occur among all such groups, as they do among taxa which tend to have similar dietary habits (e.g. Sacoglossa).

We propose the following hypothesis to explain the observations delineated above. Post-settlement mortality is size dependent; the larger the juvenile size, the greater the freedom from predation by one or more common groups of micro-carnivores (mainly small worms and crustaceans; e.g. Highsmith, 1982). Juvenile mortality is least among opisthobranch species with ametamorphic-direct development because the hatching juveniles of these species are suf-
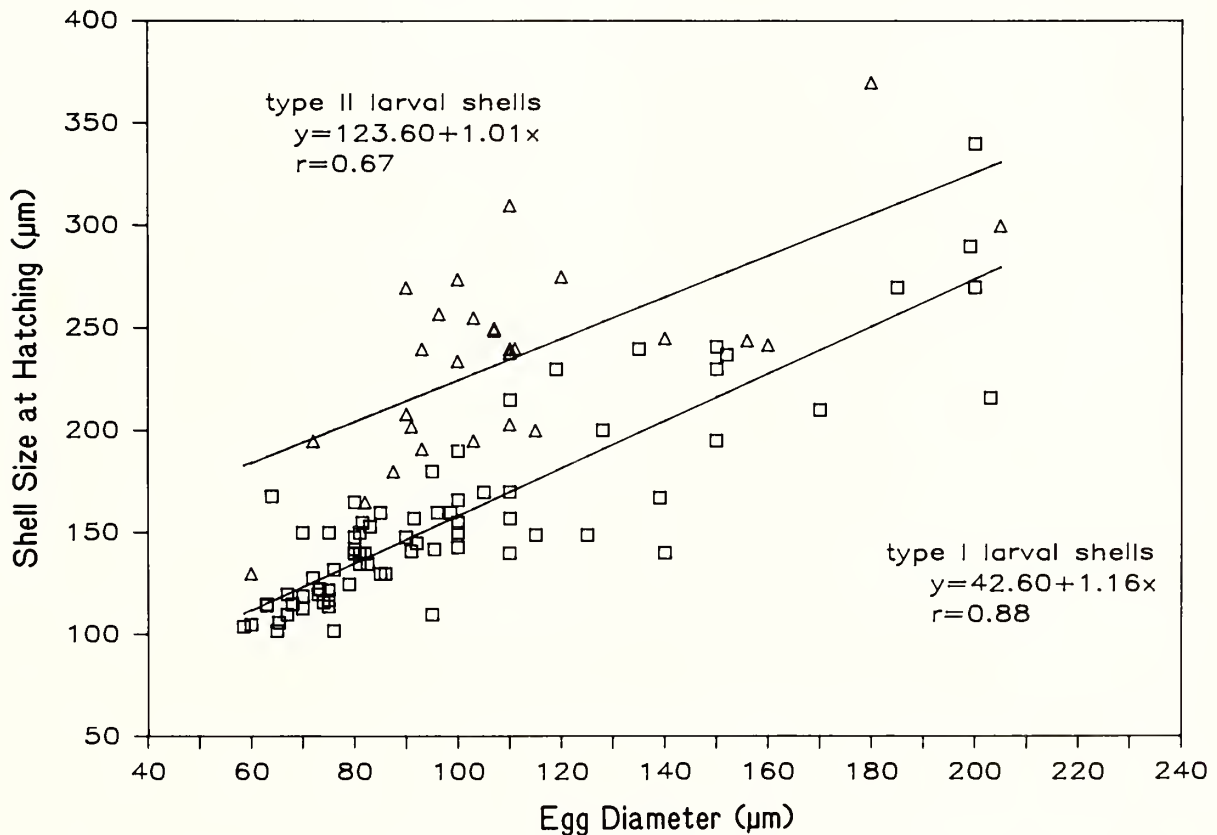


**Fig. 9.** Larval-shell length at hatching vs. egg diameter in the Nudibranchia. □,Type I larval shells (n = 75); △,Type II larval shells (n = 28).
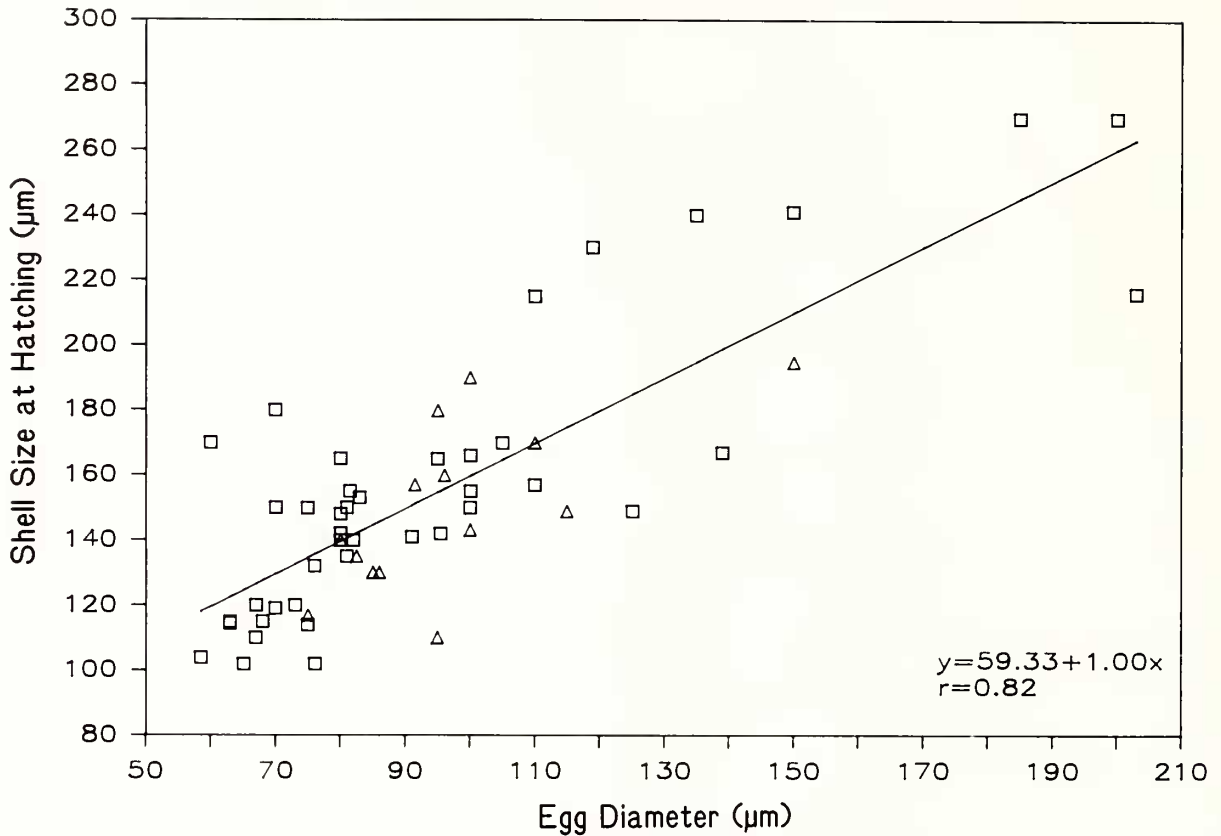
**Fig. 10.** Larval-shell length at hatching vs. egg diameter in the nudibranch suborder Doridacea (n = 57). △, family Chromodorididae (n = 14).
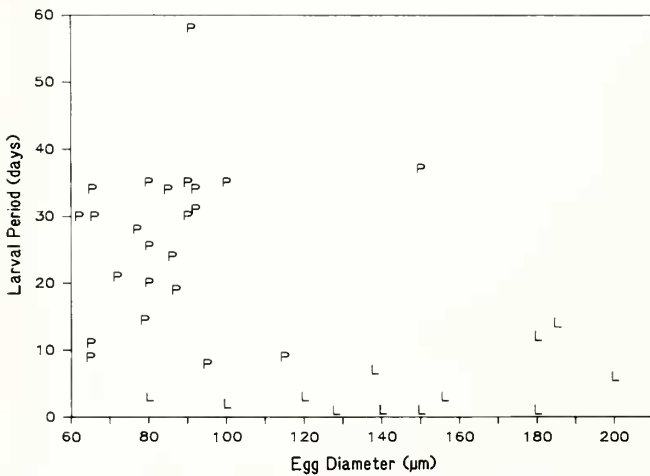


**Fig. 11.** Larval duration vs. egg diameter in the Opisthobranchia. P, species with planktotrophic development (n = 23); L, species with lecithotrophic development (n = 13).



**Fig. 12.** Larval-shell length at settlement vs. larval-shell length at hatching. □, Nudibranchia (n = 11); △, all other orders (n = 14). (Only nudibranchs with Type I shells are included).

ficiently large and well developed to avoid (by size, behavior or other factors) most micro-carnivores. The large number of larvae produced by species with pelagic-planktotrophic development are necessary to assure adult replacement after extensive mortality both in the plankton and *in early benthic stages.* Pelagic-lecithotrophic larvae, because of their brief planktic existence, suffer less mortality in the plankton, but

because their metamorphic size is small, must still be produced in sufficiently large numbers to offset high early juvenile mortality. Data to support this hypothesis are scant. Only the field studies of Sarver (1979) on the sea hare *Aplysia juliana* have documented early post-settlement mortality for an opisthobranch. Sarver calculated mortality rates in excess of 16% per day for newly settled *A. juliana.* But individuals

of this species, like most sea hares, produce hundreds of millions of offspring; its success is indicated by its distribution throughout tropical and subtropical seas of the world, and even into temperate regions such as Japan. This hypothesis predicts a great reduction in numbers of offspring in the shift from metamorphic to ametamorphic direct development. However, life-time fecundity data are not sufficiently abundant to test this prediction.

What determines the developmental mode of any individual opisthobranch species? Assuredly, there is no single answer. Given the preponderance of species with planktotrophic larvae (more than 70% of all opisthobranchs), we assume that this is the primitive mode for the group, an assumption strengthened by the unlikelihood of evolution from direct development to larviparous development (Strathmann, 1978b). Thus the evolutionary direction will be toward lecithotrophic-planktic development and from there to direct development. The most evolved forms, in terms of this life history adaptation, will be those with ametamorphic direct development. It is probable that the selective pressures leading away from planktotrophic development have not been the same across all opisthobranch species.

Selection can occur at any life-history stage. If mortality is too great in the pelagic phase, that phase can be reduced or eliminated. For example, it is possible that direct development evolved in some species in response to a brief and unreliable polar phytoplankton season, as suggested by Thorson (1950). Intense predation on early juveniles could have selected for increased size, which we have shown to be limited by pelagic development. Thus direct development evolves. Finally, any process that restricts adult size could also limit fecundity and thus influence the evolution of lecithotrophic or direct development. In some cases, a predatory opisthobranch could have adapted to a relatively short-lived prey (e.g. some hydrozoans) by itself becoming short-lived in order to grow to maturity and reproduce before the prey is exhausted. The adaptation will almost certainly include a considerable reduction in predator size, and thus, fecundity. Under these conditions, larger, lecithotrophic eggs will be favored for reasons discussed above. If prey are not too patchy, pelagic larvae could be dispensable, and the reduced fecundity related to small size will be further compensated by the production of still larger, directly developed offspring with a concomitant reduction in both larval and juvenile mortality. In other cases, competition could have restricted the growth of a species and thus reduced its reproductive output to the point where it could not successively replace itself via a larviparous mode (an argument made
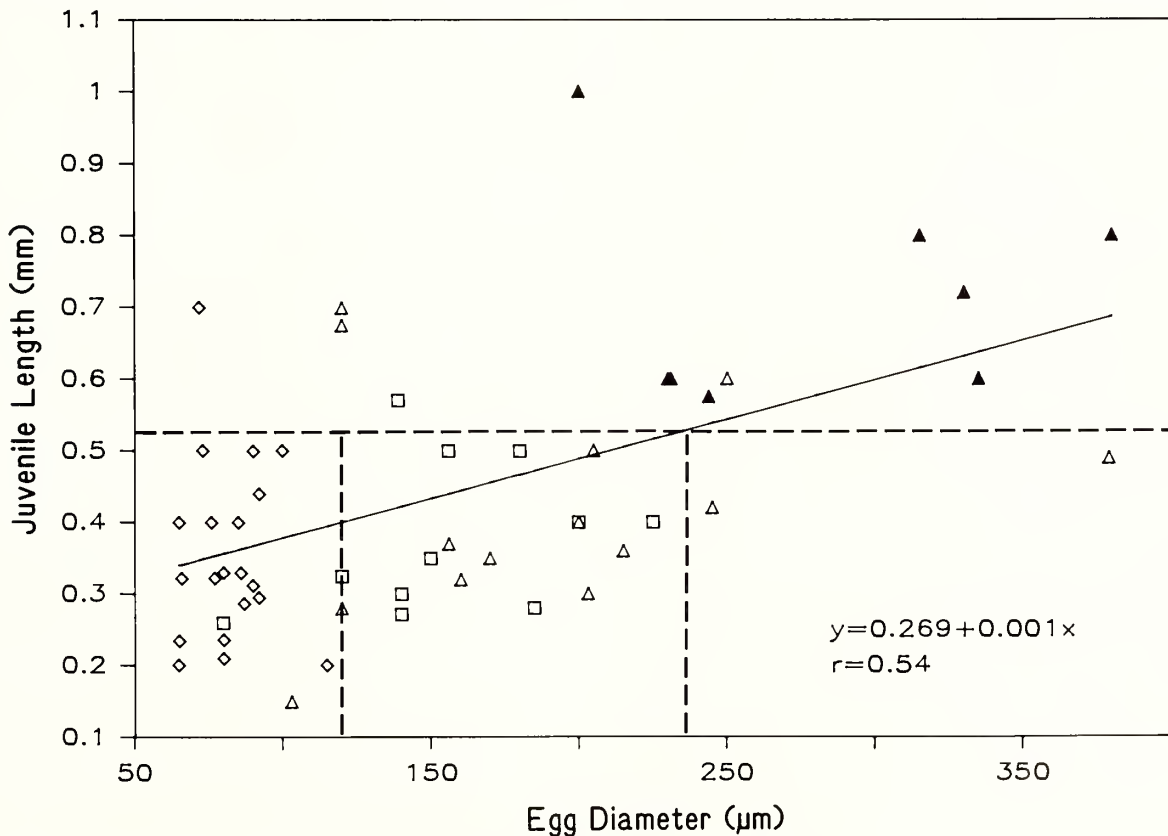


**Fig. 13.** Length of post-metamorphic juveniles vs. egg diameter. ◇, species with planktotrophic larvae (n = 21); □, species with lecithotrophic larvae (n = 11); △, species with metamorphic direct development (n = 14); ▲, species with ametamorhpic direct development (n = 8). The vertical dashed lines emphasize the egg-size limits of species with the planktotrophic and lecithotrophic development. The horizontal dashed line indicates the upper limit of juvenile length for most species which have a larval shell in their development.

Table 4. Egg size, juvenile size and adult size for directly developing opisthobranchs.

| Species | Egg. Diam. | Juv. L. | Adult L. | Dev.[1] | Reference |
|---|---|---|---|---|---|
| **Nudibranchia** | | | | | |
| *Trippa spongiosa* (Kelaart) | 200 μm | 400 μm | 55 mm | M | Gohar and Soliman (1967)[2] |
| *Casella obsoleta* (Rüppell and Leuckart) | 315 | 800 | 46 | A | Gohar and Soliman (1967)[2] |
| *Cadlina laevis* (Linnaeus) | 380 | 800 | 32 | A | Thompson (1967)[2] |
| *Chromodoris loringi* (Angas) | 330 | 720 | 15 | A | Thompson (1972)[2] |
| *Hypselodoris bennetti* (Angas) | 231 | 600 | 30 | A | Thompson (1972)[2]; Rose (1981)[2] |
| *Glossodoris gracilis* von Rapp | 244 | 575 | 36 | A | Gantès (1962) |
| *Dendrodoris miniata* (Alder and Hancock) | 215 | 360 | 28 | M | Thompson (1975); Rose (1981)[2] |
| *Doriopsilla pharpa* Marcus | 203 | 300 | 25 | M | Eyster and Stancyk (1981)[2] |
| *Okadaia elegans* Baba | 230 | 600 | <5 | A | Baba (1937)[2] |
| *Cuthona granosa* (Schmekel) | 120 | 280 | 11 | M | Schmekel and Portmann (1982) |
| *C. nana* (Alder and Hancock) | 160 | 320 | 28 | M | Rivest (1978)[2] |
| *C. pustulata* (Alder and Hancock) | 205 | 500 | 20 | M | Roginskaya (1962)[2] |
| *Tenellia pallida* (Nordmann) | 103 | 150 | 3 | M | Eyster (1979)[2] |
| *Dermatobranchus striatellus* Baba | 170 | 350 | 10 | M | Hamatani (1967)[2] |
| **Cephalaspidea** | | | | | |
| *Runcina ferruginea* Kress | 335 | 600 | 4 | A | Kress (1977)[2] |
| *R. setoensis* Baba | 250 | 600 | <7 | M | Baba and Hamatani (1959)[2] |
| *Retusa obtusa* (Montagu) | 245 | 421 | 10 | M | Smith (1967)[2] |
| *Philine gibba* Strebel | 379 | 490 | 12 | M | Seager (1979)[2] |
| **Sacoglossa** | | | | | |
| *Acteonia cocksi* Alder and Hancock | 200 | 1000 | 6 | A | Chia (1971) |
| *Elysia timida* Risso | 120 | 700 | 12 | M | Rahat (1976)[2] |
| *Oxynoe azuropunctata* Jensen | 120 | 675 | 40 | M | Jensen (1980) |
| **Anaspidea** | | | | | |
| *Phyllaplysia taylori* Dall | 150 | 370 | 45 | M | Bridges (1975)[2] |

[1]Development; M = metamorphic; A = ametamorphic. [2]Cited in Hadfield and Switzer-Dunlap, 1984.

for starfish by Menge, 1975).

Are these suggested explanations for the occurrence of lecithotrophic or direct development "pie arguments"? No, in that there are no clear and predictable effects on settling size or reproductive investment per egg associated with the different developmental modes as predicted by the pie arguments. The advantage provided by a shift from planktotrophy to lecithotrophy is a decrease in larval mortality due to a shorter planktic period (see Fig. 11). A shift to direct development (especially ametamorphic direct development) provides a further advantage, that of reduced juvenile mortality due to larger juvenile size. Where the pie arguments fail for opisthobranchs is in explaining the large numbers of minute forms that succeed with planktotrophy and the large animals that have lecithotrophic or direct development. To further sort out these potential explanations critical information is needed on average lifespans, life-time fecundities, developmental modes, larval durations, and weights of newly metamorphosed juveniles for large numbers of species with an emphasis on closely related groups living in sympatry and separated across latitudinal clines.

## CONCLUSIONS

The developmental (embryonic plus larval) period for any opisthobranch species is undoubtedly under strong genetic constraints. These determine egg size (and thus hatching size), larval shell type (and thus larval growth pattern), growth rate (which is further modulated by temperature and food abundance), and settling size (which seems to be limited at a high phylogenetic level for species with a genuine larva). These factors are all important in determining the age at which larvae become metamorphically competent. For most opisthobranchs the precompetent larval period does not greatly exceed one month.

Once a larva is metamorphically competent, the duration of the larval period is determined by the availability of appropriate settlement substrata. Opisthobranch veligers (both planktotrophic and lecithotrophic) have been shown experimentally to be able to extend their larval periods considerably in the absence of settlement inducing substrata (Kempf, 1981; Paige, 1986). Facultative feeding increases the capacity for prolonged planktic existence in lecithotrophic species (Kempf and Hadfield, 1985).

Competent larvae of opisthobranchs settle in response to a variety of settlement cues ranging from specific soluble or adsorbed chemicals to common marine bacteria and fungal films. Species with highly specific food requirements generally settle in response to chemical cues arising from the food substance. Species with less specific food requirements settle in response to more general environmental characteristics associated with an appropriate habitat or food item.

If there is a "strategy" for reproductive mode in most species, it is to maintain recruitment potential as high as possible throughout the broadest appropriate time of the year (i.e. when food is available) (Hadfield and Switzer-Dunlap,

**Table 5.** Sources of data for opisthobranchs (see also Hadfield and Switzer-Dunlap, 1984).

| Species | Egg Size | Embryonic Develop. | Larval Develop. | Hatching Size | Settling Size | References |
|---|---|---|---|---|---|---|
| Nudibranchia | | | | | | |
| *Acanthodoris brunnea* MacFarland | X | X | | X | | Strathmann, pers. comm.** |
| *A. hudsoni* MacFarland | X | X | | | | Hurst, 1967; Strathmann, pers. comm. |
| *A. nanaimoensis* O'Donoghue | | X | | X | | Hurst, 1967 |
| *A. pilosa* (Müller)* | X | X | X | X | | Strathmann, pers. comm. |
| *Adalaria* sp. | X | X | | X | | Goddard, 1984 |
| *Aegires albopunctatus* MacFarland | X | | | | | Strathmann, pers. comm. |
| *A. punctilucens* (d'Orbigny) | X | X | | | | Schmekel and Portmann, 1982 |
| *A. sublaevis* Odhner | X | X | | | | Schmekel and Portmann, 1982 |
| *Aldisa binotata* Pruvot-Fol | X | | | | | Millen and Gosliner, 1985 |
| *A. cooperi* Robilliard and Baba | X | X | | | | Millen and Gosliner, 1985 |
| *A. pikokai* Bertsch and Johnson | X | | | | | Millen and Gosliner, 1985 |
| *A. sanguinea* Cooper | X | | | | | Millen and Gosliner, 1985 |
| *A. tara* Millen | X | X | X | | | Millen and Gosliner, 1985 |
| *Ancula pacifica* MacFarland | X | X | | X | | Goddard, 1984 |
| *Anisodoris nobilis* MacFarland | X | X | | X | | Goddard, 1984 |
| *Antonietta luteorufa* Schmekel | X | X | | | | Schmekel and Portmann, 1982 |
| *Archidoris odhneri* MacFarland | | X | | X | | Hurst, 1967 |
| *A. pseudoargus* (von Rapp)* | X | X | X | X | X | Schmekel and Portmann, 1982; Todd and Havenhand, 1985 |
| *Armina californica* (Cooper) | X | X | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *A. maculata* Rafinesque | X | | | | | Schmekel and Portmann, 1982 |
| *Babaina* sp. | X | X | X | | | Boucher, 1983 |
| *Cadlina modesta* MacFarland | X | X | | X | | Goddard, 1984 |
| *Calma glaucoides* (Alder and Hancock) | X | | | | | Schmekel and Portmann, 1982 |
| *Calmella cavolini* (Verany) | X | | | | | Schmekel and Portmann, 1982 |
| *Catriona gymnota* (Couthouy) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. maua* Marcus and Marcus | | X | | | | Schmekel and Portmann, 1982 |
| *Chromodoris* sp. E6 | X | X | | X | | Boucher, 1983 |
| *Chromodoris* sp. E57 | X | X | | X | | Boucher, 1983 |
| *C. albopunctatus* (Garrett) | X | X | X | X | | Boucher, 1983 |
| *C. inornata* Pease | X | X | X | X | | Boucher, 1983 |
| *C. krohni* (Verany) | X | | | | | Schmekel and Portmann, 1982 |
| *C. luteopunctata* (Gantés) | | | | X | | Edmunds, 1982 |
| *C. tryoni* (Garrrett) | X | X | X | X | | Boucher, 1983 |
| *Cratena peregrina* (Gmelin) | X | X | | | | Schmekel and Portmann, 1982 |
| *Crimora coneja* Marcus | X | X | | X | | Goddard, 1984 |
| *C. papillata* Alder and Hancock | X | X | | | | Schmekel and Portmann, 1982 |
| *Cumanotus beaumonti* (Eliot) | | | | X | | Hurst, 1967 |
| *Cuthona albocrusta* MacFarland | | X | | X | | Hurst, 1967 |
| *C. albopunctata* (Schmekel) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. caerulea* (Montagu) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. cocoachroma* (Williams and Gosliner) | X | X | | X | | Goddard, 1984 |
| *C. columbiana* (O'Donoghue) | X | X | | X | | Goddard, 1984 |
| *C. divae* (Marcus) | X | X | | X | | Goddard, 1984 |
| *C. genovae* (O'Donoghue) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. granosa* (Schmekel)* | X | X | X | | | Schmekel and Portmann, 1982 |
| *C. ilonae* (Schmekel) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. ministriata* (Schmekel) | X | X | | | | Schmekel and Portmann, 1982 |
| *C. ocellata* (Schmekel) | X | | | | | Schmekel and Portmann, 1982 |
| *C. poritophages* Rudman | | X | X | | | Rudman, 1979 |
| *C. pustulata* (Alder and Hancock)* | X | X | X | | | Gosliner and Millen, 1984 |
| *Dendrodoris krebsii* (Mörch)* | X | | X | | | DeFreese and Clark, 1983 |

(continued)

**Table 5.** (continued)

| Species | Egg Size | Embryonic Develop. | Larval Develop. | Hatching Size | Settling Size | References |
|---|---|---|---|---|---|---|
| | | | Data on: | | | |
| *D. nigra* Stimpson* | X | X | X | X | | Rose, 1985 |
| *Dendronotus diversicolor* Robilliard | X | X | | | | Robilliard, 1970; Strathmann, pers. comm. |
| *D. frondosus* (Ascanius)* | X | X | X | X | | Williams, 1971 |
| *D. iris* Cooper | X | X | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *Diaphana californica* Dall | X | X | | X | | Goddard, 1984 |
| *Dicata odhneri* Schmekel | X | X | | | | Schmekel and Portmann, 1982 |
| *Dirona albolineata* Cockrell and Eliot | X | | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *D. aurantia* Hurst | | X | | X | | Hurst, 1967 |
| *Discodoris heathi* MacFarland | X | X | | X | | Goddard, 1984 |
| *D. maculosa* (Bergh) | X | | | | | Schmekel and Portmann, 1982 |
| *D. sandiegensis* (Cooper) | | X | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *Doris ocelligera* (Bergh) | X | X | | | | Schmekel and Portmann, 1982 |
| *Doto acuta* Schmekel and Kress | X | X | | | | Schmekel and Portmann, 1982 |
| *D. amyra* Marcus | X | X | | X | | Goddard, 1984 |
| *D. coronata* (Gmelin)* | X | X | X | X | | Schmekel and Portmann, 1982 |
| *D. doerga* Marcus and Marcus | X | X | | | | Schmekel and Portmann, 1982 |
| *D. kya* Marcus | X | X | | X | | Goddard, 1984 |
| *D. paulinae* Trinchese | X | X | | | | Schmekel and Portmann, 1982 |
| *D. rosea* Trinchese | | X | | | | Schmekel and Portmann, 1982 |
| *Embletonia pulchra faurei* (Alder and Hancock) | X | X | | | | Schmekel and Portmann, 1982 |
| *Eubranchus exiguus* (Alder and Hancock)* | X | X | X | X | | Schmekel and Portmann, 1982 |
| *E. olivaceus* (O'Donoghue) | | X | | X | | Hurst, 1967 |
| *E. rustyus* (Marcus) | X | X | | X | | Goddard, 1984 |
| *Facelina dubia* Pruvot-Fol | | X | | | | Schmekel and Portmann, 1982 |
| *F. fusca* Schmekel | X | X | X | | | Schmekel and Portmann, 1982 |
| *F. punctata* (Alder and Hancock) | X | | | | | Schmekel and Portmann, 1982 |
| *Fiona pinnata* (Eschscholtz) | X | X | | | | Schmekel and Portmann, 1982 |
| *Flabellina affinis* (Gmelin) | | X | | | | Schmekel and Portmann, 1982 |
| *F. fusca* (O'Donoghue) | | | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *F. salmonacea* (Couthouy)* | X | X | X | | | Kuzirian, 1979; Eyster, 1985 |
| *F. trilineata* O'Donoghue | X | X | | X | | Bridges and Blake, 1972; Strathmann, pers. comm. |
| *F. verrucosa* (Sars) | | X | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *Glossodoris bilineata* Pruvot-Fol | | X | | X | | Gantès, 1962 |
| *G. gracilis* von Rapp | X | X | | | | Gantès, 1962 |
| *G. luteopunctata* Gantès | | X | | X | | Gantès, 1962 |
| *Goniodoris castanea* Alder and Hancock | X | X | | | | Schmekel and Portmann, 1982 |
| *Gymnodoris* sp. | X | X | | X | | Boucher, 1986 |
| *G. striata* Eliot | X | X | X | X | | Boucher, 1986 |
| *Hallaxa chani* Gosliner and Williams | X | X | | X | | Goddard, 1984 |
| *Hancockia uncinata* (Hesse) | | X | | | | Schmekel and Portmann, 1982 |
| *Hoplodoris nodulosa* (Angas)* | X | X | X | X | | Rose, 1983 |
| *Hypselodoris messinensis* (von Ihering) | X | | | | | Schmekel and Portmann, 1982 |
| *Laila cockerelli* MacFarland | X | X | | X | | Goddard, 1984 |
| *Limenandra nodosa* Haefelfinger and Stamm | X | X | | | | Schmekel and Portmann, 1982 |

(continued)

**Table 5.** (continued)

| Species | Egg Size | Embryonic Develop. | Larval Develop. | Hatching Size | Settling Size | References |
|---|---|---|---|---|---|---|
| | | | Data on: | | | |
| *Melibe fimbriata* Alder and Hancock | X | X | X | | | Thompson and Crampton, 1984 |
| *M. leonina* (Gould)* | X | X | X | X | X | Bickell and Kempf, 1983 |
| *Miamira sinuata* (van Hasselt) | X | X | X | X | | Boucher, 1983 |
| *Onchidoris* sp. | X | X | | X | | Goddard, 1984 |
| *O. muricata* (Müller)* | X | X | X | X | X | Goddard, 1984; Todd and Havenhand, 1985 |
| *O. neapolitana* (Delle Chiaje) | | X | | | | Schmekel and Portmann, 1982 |
| *Peltodoris atromaculata* Bergh | X | | | | | Schmekel and Portmann, 1982 |
| *Phestilla sibogae* Bergh* | X | X | X | X | | Hadfield and Switzer-Dunlap, 1984 |
| *Phylliroe bucephala* Péron and Lesueur | X | X | | | | Schmekel and Portmann, 1982 |
| *Piseinotecus sphaeriferus* (Schmekel) | X | X | | | | Schmekel and Portmann, 1982 |
| *Platydoris scabra* (Cuvier) | X | X | X | X | | Soliman, 1978 |
| *Polycera quadrilineata* (Müller)* | X | X | X | X | | Schmekel and Portmann, 1982 |
| *P. zosterae* O'Donoghue | X | | | X | | Strathmann, pers. comm. |
| *Polycerella emertoni* Verrill | X | X | | | | Schmekel and Portmann, 1982 |
| *Precuthona divae* Marcus | X | X | | X | | Goddard, 1984 |
| *Pteraeolidia ianthina* (Angas)* | X | X | X | X | | Rose and Hoegh-Guldberg, 1982 |
| *Scyllaea pelagica* Linnaeus | X | | X | | | DeFreese and Clark, 1983 |
| *Sebradoris crosslandi* (Eliot) | X | X | X | X | | Soliman, 1980 |
| *Tergipes tergipes* (Forskal)* | X | | | | | Schmekel and Portmann, 1982 |
| *Tethys fimbria* Linnaeus | X | | | | | Schmekel and Portmann, 1982 |
| *Thecacera pennifera* (Montagu) | X | | | | | DeFreese and Clark, 1983 |
| *Thordisa filix* Pruvot-Fol | X | X | | | | Schmekel and Portmann, 1982 |
| *Thorunna clitonata* (Bergh) | X | X | X | X | | Boucher, 1983 |
| *T. decussata* (Risbec) | X | X | X | X | | Boucher, 1983 |
| *T. norba* (Marcus and Marcus) | X | X | X | X | | Boucher, 1983 |
| *Trapania maculata* Haefelfinger | X | | | | | Haefelfinger, 1960 |
| *Triopha catalinae* (Cooper) | X | X | | X | | Strathmann, pers. comm. |
| *Tritonia festiva* (Stearns) | X | X | | X | | Goddard, 1984 |
| *Tritoniopsis cincta* Pruvot-Fol | | X | | | | Schmekel and Portmann, 1982 |
| Sacoglossa | | | | | | |
| *Aplysiopsis smithi* (Marcus) | X | X | | X | | Goddard, 1984 |
| *Bosellia mimetica* Trinchese* | X | X | | | | Schmekel and Portmann, 1982 |
| *Caliphylla mediterranea* Costa* | X | X | | | | Schmekel and Portmann, 1982 |
| *Calliopaea bellula* d'Orbigny | | X | | | | Schmekel and Portmann, 1982 |
| *Costasiella ocellifera* (Simroth) | X | | | | | DeFreese and Clark, 1983 |
| *Cyerce cristallina* (Trinchese) | X | X | | | | Schmekel and Portmann, 1982 |
| *Elysia* sp. | X | | X | | | DeFreese and Clark, 1983 |
| *E. chlorotica* (Gould)* | X | X | | X | | West, Harrigan and Pierce, 1984 |
| *E. hedgpethi* (Marcus)* | X | X | | X | | Strathmann, pers. comm. |
| *E. hopei* (Marcus) | X | X | X | X | | Thompson and Salghetti-Drioli, 1984 |
| *E. patina* Marcus | X | | X | | | DeFreese and Clark, 1983 |
| *E. subornata* (Verrill) | X | | | | | DeFreese and Clark, 1983 |
| *E. tuca* Marcus* | X | | X | | | DeFreese and Clark, 1983 |
| *Ercolania funerea* (Costa) | X | X | | | | Schmekel and Portmann, 1982 |
| *E. fuscata* (Gould) | X | | X | | | DeFreese and Clark, 1983 |
| *Hermaea bifida* (Montagu) | X | | X | | | Schmekel and Portmann, 1982 |
| *Lobiger serradifalci* (Calcara) | | X | | | | Schmekel and Portmann, 1982 |
| *Olea hansineensis* Agersborg | | X | | X | | Strathmann, pers. comm. |
| *Placida cremoniana* (Trinchese) | | X | | | | Schmekel and Portmann, 1982 |
| *P. viridis* (Trinchese)* | | X | | | | Schmekel and Portmann, 1982 |
| *Stiliger fuscovittatus* Lance | | | | X | | Strathmann, pers. comm. |
| *Tridachia crispata* Mörch* | | X | X | | | DeFreese and Clark, 1983 |

(continued)

**Table 5.** (continued)

| Species | Egg Size | Embryonic Develop. | Larval Develop. | Hatching Size | Settling Size | References |
|---|---|---|---|---|---|---|
| | | | Data on: | | | |
| Cephalaspidea | | | | | | |
| *Aglaja ocelligera* (Bergh) | | X | X | X | | Hurst, 1967 |
| *Chelidonura* sp. | | | X | | | DeFreese and Clark, 1983 |
| *Gastropteron pacificum* Bergh | | X | | | | Hurst, 1967 |
| *Haminoea* sp. | | X | X | | | Strathmann, pers. comm. |
| *H. antillarum* (d'Orbigny) | X | | | | | DeFreese and Clark, 1983 |
| *H. vesicula* (Gould) | X | X | | X | | Hurst, 1967; Strathmann, pers. comm. |
| *Melanochlamys diomedea* (Bergh) | | X | X | X | | Hurst, 1967 |
| Anaspidea | | | | | | |
| *Phyllaplysia engeli* Marcus* | X | | X | | | DeFreese and Clark, 1983 |
| Notaspidea | | | | | | |
| *Berthella californica* (Dall) | X | X | | X | | Goddard, 1984 |

*Species that were previously listed in Hadfield and Switzer-Dunlap, 1984, for which new references are available.
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1984). Thus when short lived, sessile and rapidly growing foods (hydrozoans, bryozoans, algae) become available, larvae are available to take advantage of them. To accomplish this, most species are limited to smaller juveniles due to a not-understood limitation on the upper size of planktic opisthobranch veligers. The numbers of eggs (and thus larvae) produced must be sufficiently high to offset both larval mortality and increased juvenile mortality (relative to that of ametamorphically directly developing species). Species with direct development are far more limited in their spatial dispersal, but their large birth size imbues them with a greater likelihood of survival.

The puzzle remains as to why we often find all three developmental modes occurring among sympatric opisthobranchs, often even among family mates or congeners with the same or similar food requirements. Alas, shell-less opisthobranchs fossilize badly and for most we shall never know the place or time of their evolutionary divergence. However, we have no valid reason to assume that species currently found together evolved in sympatry or under the conditions in which they are now found. These limitations will always restrict our ability to construct predictive models for the pattern of reproduction of any opisthobranch species or for its larval longevity.

Data on opisthobranch larval settling size and on the allocation of energy to reproduction by adults do not support the predictions of "pie arguments", often suggested as an explanation for species-specific developmental mode. Settling sizes of larvae vary widely within and between planktotrophy, lecithotrophy and direct development. Energy allocated to reproduction by adults cannot be predicted from developmental mode in the few species for which data are available. In addition, pie argument predictions correlating egg size (or hatching size) with settling size or with larval duration are not supported by the data.

Given the poor value of most quantifiable life-history traits (egg size, reproductive effort, adult size, food type) in predicting developmental mode, we suggest that crucial selective pressures often occur during planktic larval phases, at the time of recruitment, and during early juvenile development.

## ACKNOWLEDGMENTS

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